

DISCUSSION

Levels of herbivory were higher in the gaps than in the forest understory, which suggests that understory trees are better defended against herbivores than gap trees of the same species just a few meters away. These differences are probably not due to genetic differences, so it appears that patterns of phenotypic plasticity in antiherbivore defenses across light gradients at Monteverde match the patterns of genetic variation in plant defenses (Coley 1985). This phenotypic plasticity can be interpreted as an adaptive adjustment of allocation strategies (optimal allocation model) by the same reasoning that Coley (1985) used to explain genetic differences between gap species and understory species. In contrast, the observed phenotypic pattern in herbivory is exactly the opposite that would be expected under models of phenotypic variation in plant defenses that emphasize physiological constraints, rather than optimal allocation (carbon surplus model).

An alternative explanation for the correlation between gap position and herbivory level is that herbivorous arthropods are more abundant in treefall gaps than in the forest canopy (Berry 1994). This could result if plants that occur in gaps experience higher herbivory than plants of the same species that occur in understory habitats, regardless of their allocation to growth vs. defense. Direct measurements of arthropod abundance and/or plant secondary metabolites would be useful in distinguishing between these very different explanations for the differences in leaf herbivory between gaps and understory.

R. spicata experienced the highest herbivory levels in each position along the light gradient, indicating that it might allocate lower amounts of energy to defense than the other species. Based upon this pattern, Coley's model of interspecific variation in plant defenses would predict that *R. spicata*

also has a higher maximum growth rate than the other species and is more strongly restricted to gaps than the other species.

Phenotypic patterns in herbivores from canopy to gap center were strikingly similar between species. This gradient in herbivore pressure across the light gradient could influence patterns in species composition from the canopy to the gap, and therefore influence the diversity of plant life within the forest as a whole.

LITERATURE CITED

- Berry, M. E., A.N. Swanson, and D.B. Zug. 1994. A comparison of arthropod abundance in gap and understory habitats in a montane wet forest. Pp. 43-45 in J.W. Bykowski, editor, Dartmouth Studies in Tropical Ecology 1994. Dartmouth College, Hanover, NH.
- Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53: 209-233.
- Coley, P. D., J.P. Bryant, and F.S. Chapin, III. 1985. Resource availability and plant anti-herbivore defense. *Science* 230: 895-899.
- Coley, P. D. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74: 531-536.
- Coley, P.D. 1993. Gap size and plant defenses. *Tree* 8: 1-2.
- Sagers, C. L., and P.D. Coley. 1995. Benefits and costs of defense in a neotropical shrub. *Ecology* 76: 1835-1843.

EFFECTS OF LIGHT ON THE REPRODUCTIVE DEVELOPMENT OF *BEGONIA INVOLUCRATA*

MICHAEL D. FOOTE, KATHERINE W. MANARAS, AND SARAH E. LAPLANTE

Abstract : Reproductive development of *Begonia involucrata* may be influenced by small scale variation in light availability. The probability that a begonia individual would be flowering increased with increasing openness of canopy at 1500 m and 1600 m sites, but was unrelated to light at 1700 m. The probability of flowering increased dramatically as openness of canopy increased from 10 - 20%. Changes in cloud cover at Monteverde, which may be an indirect effect of climate change (Pounds et al. 1999), could impact the reproductive success and therefore abundances of begonia populations in this cloud forest.

Key Words: canopy cover, microhabitat, resource partitioning

INTRODUCTION

Light is an essential resource for plant growth and reproduction, but is distributed unevenly throughout the forest understory. Hundreds of plant species compete for light and other more coarsely distributed resources in the understory of the Monteverde tropical cloud forest. Much research has studied the effects of large treefall gaps on forest dynamics, but the effects of smaller scale variations in canopy cover have not been as thoroughly explored. It is known that plant growth rates are accelerated in treefall gaps, so light may be influential to growth and reproduction on finer spatial scales as well.

In the cloud forest, where treefall gaps are the natural disturbance regime, many species are characteristically associated with particular light conditions. Many early successional species, for example, are associated with the high light levels in gaps. *Begonia involucrata* is distributed over a wide range of light conditions in the forests of Monteverde. Some individuals are in high light, while others are in very shaded areas. At the start of the dry season, in late January, begonia individuals varied greatly in their developmental stage (some were flowering, some were producing flower buds, and others had no flowers or buds). We hypothesized that begonia reproductive stage is a function of small scale variations in light experienced

by individual plants and that the probability of flowering increases with local light regimes. We further predicted that the importance of light would vary among sites that differed in other abiotic factors, such as temperature, nutrient availability, and cloud cover.

METHODS

This study was conducted in the Monteverde cloud forest, Costa Rica, on 21 - 23 January 2000. We sampled begonia individuals along ≈ 35 m of trail at each of 3 elevations (1500, 1600, and 1700 m; $n = 38, 38,$ and 38 individuals, respectively). For each plant, we recorded its most advanced stage of reproductive development (no reproductive development, floral buds, or flowers/fruit). We estimated light availability as the percent open canopy above each individual as measured with a spherical densiometer.

For every site, we used logistic regressions to estimate the relationship between percent open canopy experienced by each plant and the probability that a plant would be flowering and/or fruiting.

RESULTS

Sites differed in the proportion of plants that were flowering: 25% of 38 plants at 1500 m were flowering, 19% of 38 plants at 1600 m were flowering, and 0% of 38 plants

at 1700 m were flowering (Chi-square = 24.80, $df = 2$, $p < 0.001$). Percent open canopy was higher at 1500 m than either 1600 or 1700 m: mean \pm SD = 11.1 ± 5.8 , 7.3 ± 3.1 , 7.3 ± 2.7 , respectively ($F_{2, 104} = 10.41$, $p < 0.001$, Tukey-Kramer comparisons). The probability of flowering increased with increasing light at both 1500 and 1600 m, but was unrelated to light at 1700 m (Table 1). At both of the lower sites, the probability of flowering increased dramatically as the percent open canopy increased from 10 to 20% (Fig. 1).

TABLE 1. Results of logistic regressions testing for effects of canopy openness on probability of flowering for begonia populations at each of three elevations. Figure 1 shows corresponding logistic functions.

elevation (m)	n	χ^2	P
1500	38	8.12	0.004
1600	31	3.78	0.052
1700	37	-	-

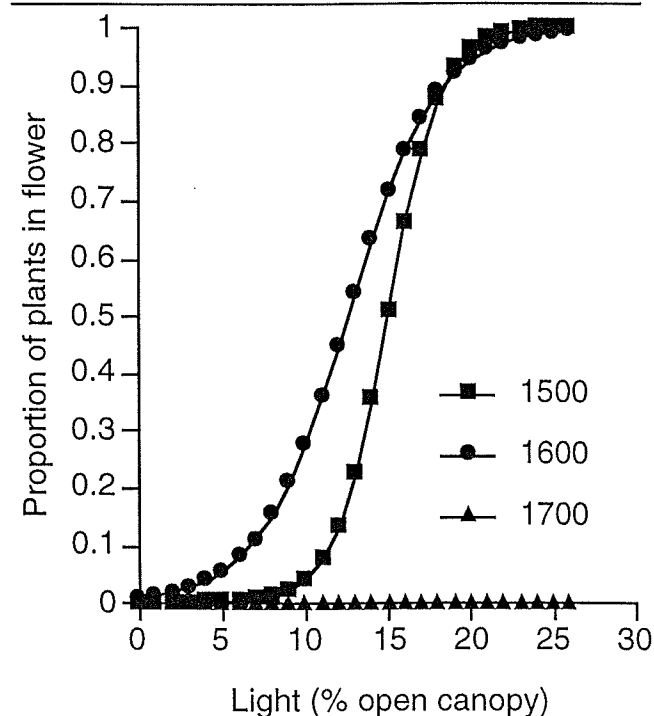


Figure 1. Logistic functions describing the response of *Begonia involucreta* to canopy structure at three elevations (1500, 1600, and 1700 m) within the montane cloud forest near Monteverde, Costa Rica. See Table 1 for associated statistics.

DISCUSSION

At two of three sites, begonia reproductive development was a function of microsite light availability. Within sites, the probability of flowering increased with increasing light availability, indicating that light is a limiting resource for begonias. However, variation in flowering among sites could not be easily explained by percent open canopy. The frequency distribution of canopy cover was no different between sites at 1600 m and 1700 m, but there were many flowering plants at 1600 m and none at 1700 m. Temperatures and nutrient availability tend to be lower at higher elevations, and thus might be more limiting than light at 1700 m. Also, canopy cover does not necessarily provide a good comparison of light availability across sites. Cloud cover is higher at high elevations, so begonia individuals under equal canopy openings will receive lower irradiance at higher elevations than at lower elevations. However, percent canopy opening must be a good measure of light availability within sites because average cloud cover does not vary at a scale of < 35 m.

Because light is important to begonia development, any changes in light conditions at Monteverde could affect begonia populations. Specifically, changes within the range of 10–20% open canopy can have very strong effects on the probability of flowering (Fig 1). If cloud cover is tending to decrease at Monteverde due to climate change (Pounds et al. (1999), this may enhance the reproductive success of understory plant species such as *Begonia involucreta*. One consequence may be that begonias become more abundant at high elevations. Another possible consequence is that begonia populations at lower elevations become less sensitive to microsite canopy cover and more sensitive to other factors such as temperature and moisture. Future research could test for such effects of longterm climate change on *B. involucreta* at

Monteverde.

LITERATURE CITED

- Pounds, J.A., M.P.L. Fogden, and J.H. Campbell. 1999. Biological response to climate change on a tropical mountain. *Nature* 398: 611–614.